



Productivity controls macrofauna diversity in the deep northern Gulf of Mexico



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ARTICLE INFO

Keywords:

Deep Gulf of Mexico
Macrofauna
 α -diversity
Productivity-diversity relationship
Habitat heterogeneity
Mid-depth-diversity maximum

ABSTRACT

The α -diversity in two large-scale, systematic macrobenthos surveys (1983–1985 and 2000–2001) in the deep northern Gulf of Mexico (GoM) has been compared under strong vertical and horizontal productivity gradients to examine underlying factors that control the distribution of deep-sea diversity. We calculated the effective numbers of equally abundant species (Hill numbers) from 100 randomly selected individuals to examine spatial patterns of species richness and evenness. Macrofauna α -diversity was a negative parabolic function of depth; the minima occurred at high export POC flux on the upper continental slope and on the abyssal plain with extremely low input of POC; the maximum occurred at intermediate levels of macrofauna biomass and input of POC. The overall parabolic pattern of α -diversity was stable over the 20-year period and not statistically different between meso-scale depressions (e.g., basins and canyons) and their adjacent slope habitats; however, the diversity was significantly higher in the NE than the NW slope habitats. The observed Mid-Depth-Maximum (MDM) in α -diversity, we suggest, was likely a result of dynamic equilibrium between productivity and competitive exclusion. The higher diversity and productivity in the NE than the NW GoM at similar depth ranges suggests that, for the first time, the productivity-diversity relationship was observed independent of other depth-related factors. The findings provide a foundation for predicting the possible responses of diversity to climate change and anthropogenic impacts in the deep sea.

1. Introduction

Variations in the numbers of co-existing species in natural communities have puzzled ecologists for more than half a century (Hutchinson, 1959; Whittaker, 1972), but the suite of possible variables that might control biodiversity is large (Huston, 1979), with explanations remaining equivocal. On seemingly monotonous muddy sea floors, it has been suggested that biodiversity is directly related to environmental stability (Sanders, 1968) and inversely related to physiological stress (Rhoads, 1974). The premise is that the long-term stability in the deep sea minimizes niche overlap and promotes species coexistence (Hessler and Sanders, 1967). Diversity thus increases from physically dynamic shallow water habitats into the supposedly more tranquil deep sea, but this increase from shallow to deep water is reversed at intermediate depths on the continental slope, producing an inverse parabola with a ‘mid-depth maximum’ (MDM) (Rex, 1981; McClain and Schlacher, 2015; Rex and Etter, 2010). However, accumulated evidence suggests that disturbance in the deep sea is not uncommon and the “time-stability hypothesis” remains difficult to test

(McClain and Schlacher, 2015). A “patch dynamics”, in which species coexist among microhabitats and small-scale disturbance (e.g., settling detritus, megafauna feeding pits or trails), may better describe deep-sea diversity (Grassle and Maciolek, 1992; Snelgrove et al., 1996). These spatial-temporal out-of-sync patches may reduce competitive exclusion and allow colonists to coexist at different successional stages. Nevertheless, “patch dynamics” does not explain the widely recognized MDM in the deep sea.

It has been suggested that an inverse parabola is a general reaction of diversity to productivity (Rosenzweig and Abramsky, 1993), with dominance by a few species when resources are liberal, followed by a decrease in dominance as resources diminish (Huston, 1979). On the muddy ocean floor, the increase in diversity initially may be a relaxation of competitive exclusion due to diminishing supply of the rain of organic detritus with depth. This increase in diversity continues offshore until it reaches a ‘tipping point’, past which the further decline in resources leads to stochastic extinctions (e.g., Allee effect) and a loss of species (Rex and Etter, 2010; Tittensor et al., 2011; McClain and Schlacher, 2015).

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Temperature is another commonly examined factor that affects biological processes at all levels from individual metabolic rate to speciation; it probably drives latitudinal diversity patterns in most marine taxa (Roy et al., 1998; Tittensor et al., 2010). On the seafloor, a general inverse parabolic temperature-diversity relationship has also been suggested; however, such a pattern has only been revealed by meta-analysis at a global scale (Yasuhara and Danovaro, 2016). Most contemporary deep-sea studies suggest productivity (e.g., export POC flux) has more influence on diversity than temperature (McClain et al., 2012; Tittensor et al., 2011; Woolley et al., 2016) because concurrent studies covered limited temperature ranges that captured only the positive (thermal enhancement) or negative components (thermal tolerance) of the temperature-diversity parabola (Yasuhara and Danovaro, 2016). On the contrary, the food supply (e.g., export POC flux) declines drastically with depth within manageable scales of the individual studies and thus likely smothers any effect of temperature (McClain et al., 2012; Tittensor et al., 2011; Woolley et al., 2016).

In addition to energy availability (e.g., food supply & temperature), habitat heterogeneity is widely recognized as a key factor influencing diversity across multiple spatial scales (Danovaro et al., 2013; Zeppilli et al., 2016). The variations of habitat from fine scale (e.g., patch dynamics), local-scale (e.g., within habitats), meso-scale (e.g., canyon, slope, and basin etc.) to macro-scale (e.g., different margins) are likely to allow more species to coexist in a given area (Levin and Sibuet, 2012; Rex and Etter, 2010). For example, species diversity of macrofauna was found to be a positive function of sediment grain size diversity in the NW Atlantic (Etter and Grassle, 1992), presumably, due to selective utilization of sediment size by deposit feeders (McClain and Schlacher, 2015). Distinctly different diversity of macrofauna between canyon and non-canyon habitats has been attributed to organic accumulation and physical disturbance (De Leo et al., 2014; Liao et al., 2017; Vetter and Dayton, 1998). Oxygen minimum zones (OMZs) may produce a steep decline in diversity within the core of OMZs accompanied by elevated diversity and species turnover across the upper and lower boundaries of the OMZs (Gooday et al., 2010).

Quantitative investigations of macrofauna communities in the deep Gulf of Mexico (GoM) were initiated in the mid-1960's (reviewed by Rowe, 2017). Distinct vertical (depth-related) and horizontal (east-west) variation in macrobenthos abundance, biomass and composition are believed to be controlled by food availability, or the slow rain of particulate organic carbon (POC) arriving at the seafloor (Wei et al., 2012a, 2010). The majority of such export detritus is consumed and respired in the water column and thus declines with depth (Biggs et al., 2008). However, the Mississippi River runoff into the NE GoM and offshore entrainment of the river plume by meso-scale eddies also enhance surface productivity and thus produce a sharp east-west gradient in export POC flux (Biggs et al., 2008; Jochens and DiMarco, 2008; Rowe et al., 2008a). Moreover, large submarine canyons (e.g., the Mississippi and De Soto Canyons) in the NE GoM may funnel and accumulate detritus through lateral transport (Rowe et al., 2008b), which is evident by the enhanced biomass, distinct species composition and dominance of opportunistic species in the canyons (Soliman and Rowe, 2008; Wei et al., 2012a, 2010).

Despite past comprehensive macrobenthos investigations in the GoM, the macro-ecological patterns in species diversity and the generality of the MDM across multiple habitats in the northern GoM remains unclear (Rowe, 2017). The relationships between the tipping point in deep-sea macrofauna diversity and specific levels of food supply have not been described. The influence of habitat heterogeneity on the overall level of diversity remains elusive (Rowe and Kennicutt, 2008) and the collinearity between depth and potential controlling factors precludes clear understanding of what drives the diversity patterns (Rex and Etter, 2010). The non-MDM patterns that can commonly occur appear to be related to regional hotspots of food deposition (Bernardino et al., 2012), topographic complexity (Levin and Sibuet, 2012), oxygen minimum (Gooday et al., 2010; Levin, 2003), abrupt

change in thermal regime (Narayanaswamy et al., 2010), or other environmental factors (Flach and de Bruin, 1999; Tselepides et al., 2000; Włodarska-Kowalczyk et al., 2004).

The present analysis utilized the results of a large-scale, systematic macrobenthos survey in the N GoM in the 2000's (Rowe and Kennicutt, 2008). By analyzing the macrofaunal diversity patterns under strong vertical and horizontal productivity gradients, we aim to control for the strong effect of depth (by comparing samples at similar depth intervals and ranges) to understand the underlying factors that control the distribution of diversity. We illustrate the MDM and defined the diversity tipping point for the continental margin in terms of specific rates of particulate organic carbon (POC) input. We also overlapped and compared our results with historical data collected in the 1980's (Pequegnat et al., 1990) to construct a baseline condition of GoM diversity against potential human (e.g. Deepwater Horizon oil Spill in 2010) (Montagna et al., 2013) and climate change impacts within the deep ocean (Sweetman et al., 2017). In short, we tested the following null hypotheses: (1) there was no unimodal diversity-depth relationship in the N GoM; (2) habitat heterogeneity did not affect diversity between meso-scale basin vs. non-basin, canyon vs. non-canyon, (3) the NW vs. NE continental slope diversities were similar; (4) there was no discernable temporal change in overall level of diversity between the current and historical data; and (5) productivity, temperature, sediment size diversity and dissolved oxygen concentration did not affect diversity across the N GoM.

2. Methods

2.1. Sampling

Benthic macrofauna in the northern Gulf of Mexico (GoM) was sampled during the Deep Gulf of Mexico Benthos (DGOMB) program (Rowe and Kennicutt, 2008) from the shelf break from NW Florida to SW Texas out to the Sigsbee Abyssal Plain. A total of 51 locations from depths 200–3700 m (Fig. 1) were sampled in summers of 2000–2002 with a 0.2-m² GOMEX box corer (Boland and Rowe, 1991). For each core, 0.17-m² of sediments were taken (excluding subcores). At least five cores were deployed at each station and overall 271 cores were taken, which equaled over 46 m² of seafloor sampled. The top 15 cm of sediments were sieved through a 300-micrometer mesh to separate macrofauna animals from the fine mud and sand fraction. The retained material was fixed in 10% buffered formalin diluted with filtered seawater. Samples were stained with 5% Rose Bengal for at least 24 h, and then rinsed with freshwater. The stained samples were sorted into major taxonomic groups and transferred to 70% ethyl alcohol for permanent preservation and species identification. A total of 980 putative species (27% named species and 73% undescribed species) from six major macrofauna taxa (amphipods, aplacophorans, bivalves, cumaceans, isopods, and polychaetes) were identified. These six taxa represent more than 46% of the total abundance and more than 90% of the total biomass from the 39 higher taxa collected during the DGOMB program (Wei et al., 2012a).

Historical data from the Northern Gulf of Mexico Continental Slope (NGoMCS) study from 1983 to 1985 were used for comparison (Pequegnat et al., 1990). During the NGoMCS study, a smaller GOMEX box core (area = 0.06 m²) was used to sample benthic macrofauna for 45 sites (from 324 core replications) based on the same sampling procedure and sieve size. A total of 951 species from the same six major taxa were retained for this analysis.

2.2. Environmental data

Bottom temperature and dissolved oxygen were measured by standard CTD lowering (data derived from Jochens and DiMarco, 2008). Sediment grain size was measured by standard Folk (1974) settling method (data derived from Morse and Beazley, 2008). We calculated

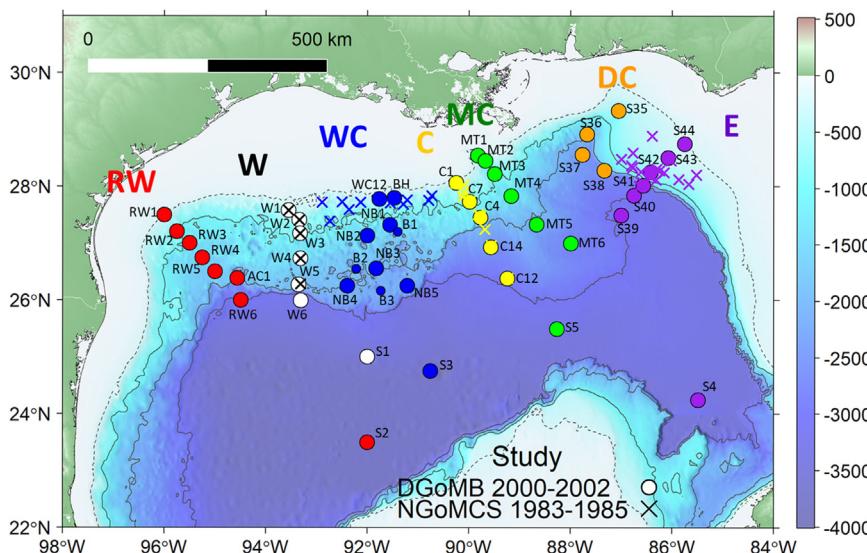


Fig. 1. Sampling sites of box cores during DGoMB (2000–2002) and NGoMCS (1983–1985) studies in the northern Gulf of Mexico (GoM). The color symbols from left to right indicate the real west (RW) slope, west (W) slope, west central (WC) slope, central (C) slope, Mississippi Canyon (MC), De Soto Canyon (DC) and east (E) slope transects, respectively. Three basin sites (B1 to B3) indicated by small blue circles. The dashed line shows the 200-m depth and solid lines show the isobaths in 1000-m increments. Note that the northwestern GoM (Transects RW, W and WC) and northeastern GoM (Transects C, MC, DC and E) are separated by Latitude 91°W. Exact coordinates and station names of each transect can be found in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

the sediment grain size Shannon diversity index from relative proportion of sand, silt and clay in the surface sediments. Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean-color data (pixel size = ~1 km²) were obtained from January 1998 to December 2002. Depth-integrated net primary production (NPP) at 51 sampling sites (catchment = 5-by-5 pixels per site) was estimated from biweekly composite averages of surface chlorophyll concentration (SST), photosynthetically available irradiance (PAR), and sea surface temperature (SST) using a Vertical General Production Model (VGPM) (Behrenfeld and Falkowski, 1997). Delivery of particulate organic carbon (POC) to the seafloor was estimated from NPP using an exponential decay model [flux (Z) = 3.523 NPP Z^{-0.734} where Z is the sample depth] (Pace et al., 1987). Detailed methods and the ocean-color data of the Gulf of Mexico sampling sites are derived from Biggs et al. (2008).

2.3. Diversity calculation

Local species diversity (α -diversity) was estimated using Hill numbers (Hill, 1973), or the effective numbers of equally abundant species (Chao and Jost, 2010). The Hill number is given by ${}^qD = (\sum_{i=1}^S p_i^q)^{1/(1-q)}$, when $q \geq 0$ and $q \neq 0$ (Eq. 1) or ${}^qD = \exp(-\sum_{i=1}^S p_i^q \log(p_i))$, when q approximates 1 (Eq. 2). In the equations, S is the number of species in a site and p_i is the relative abundance of i th species. The order q controls the sensitivity of qD to the relative species abundance; therefore, a larger q gives more weight to common or abundant species. For example, $q = 0$ gives equal weights to all species and thus qD is equivalent to the total number of species (Eq. 1). When $q = 1$, qD is the effective number of typical (or more abundant) species and equivalent to exponential of familiar Shannon diversity index (Eq. 2). When $q = 2$, qD is the effective number of dominant species and equivalent to inverse of familiar Simpson diversity index (Eq. 1). In this analysis, we calculated the Hill numbers for the order $q = 0$ to $q = 2$ to cover α -diversity from the richness to evenness aspects in a unified framework (Chao and Jost, 2010; Magurran, 2004). To give an absolute measure of α -diversity at a normalized sample size, we calculated mean Hill numbers from 100 randomly selected individuals based on 1000 bootstrap resamplings; therefore, our Hill number is conceptually similar to the familiar rarefaction index or expected number of species (Hurlbert, 1971; Sanders, 1968). For those samples with less than 100 observed individuals, the Hill numbers were extrapolated based on the method developed by Chao et al. (2013), assuming multinomial distribution for species abundance. The Hill Number measures effective number of equally abundant species, so it behaves like species number. For example, we can partition the Hill numbers of a total assemblage

into contributions of individual taxa (e.g. polychaetes, bivalves, etc.); therefore, Hill Numbers are more ecologically intuitive than the traditional diversity indices. For simplicity, we hereafter refer to the Hill numbers of order 0–2 from 100 randomly selected individuals as ‘species richness’, ‘exponential Shannon’ and ‘inverse Simpson’ indices throughout the paper. These are equivalent to ‘total number of species’, within habitat diversity, and dominance diversity.

2.4. Statistical analysis

We used linear mixed effect models (LME) with depth and the quadratic of depth as fixed factors to examine the average response of diversity (i.e., Hill numbers) to depth, and seven transects as random factors to estimate the amount of variation in average diversity among transects. In each LME, the variation around the intercept and slope for each transect were set to be normally distributed with a certain variance (i.e., assuming random intercept and slope). Additional LMEs adding sampling time (DGoMB vs. NGoMCS) into the fixed factor and four slope transects (W, WC, C & E) as random factors were used to examine whether the overall level of diversity in the current sampling (DGoMB) varied from that in the historical data (NGoMCS).

We used general least square (GLS) models with depth and the quadratic of depth as covariates to test whether the diversity (i.e., Hill numbers) varied between:

- (1) Basin (B) vs. non-basin (NB) slope sites;
- (2) Mississippi submarine canyon (MC) vs. central (C) slope transects;
- (3) De Soto submarine canyon (DC) vs. east (E) slope transects; and
- (4) the western (RW, W, WC) vs. eastern (C, E) slope transects (Fig. 1).

Finally, LMEs with monotonic and quadratic terms of export POC flux, temperature, dissolved oxygen and sediment Shannon diversity index as fixed factors and transects as random factors were used to examine linear relationships between diversity and environmental drivers. Before LME modeling, all environmental variables were normalized (divided by standard deviation and subtracted by the mean). The slopes and intercepts of the LMEs were set to random (normally distributed among transects). We estimated the parameter coefficients of LME by model averaging of all possible combinations of the models. The relative importance of fixed factors were estimated by summing their Akaike weights to measure the likelihood of a particular factor to be presented in the average model. Additionally, generalized additive mixed effect models (GAMM) with the same fixed and random factors were used to check the non-linearity between diversity and

environmental variables.

All statistical analyses were performed on R, version 3.4.0 (R Core Team 2017). Hill numbers were calculated using the *iNEXT* package. LME and GLS modeling used the *nlme* package. Model averaging and estimation of relative importance of independent variables used the *MuMin* package. GAMM used the *mgcv* package. GIS mapping and geospatial analysis used *raster* and *sp* packages. A significance level $\alpha = 0.05$ was applied to all statistical tests. All model residuals were checked by standard diagnostic plots (i.e., residual vs. fitted values, qq plot) for assumptions of homogeneity, independence and normal distribution, and by Moran I test, Moran I spatial correlogram and Variogram for spatial auto-correlation. The model assumptions are reasonably satisfied and spatial autocorrelation was not detected. All model outputs and validations can be found in File S1.

3. Results

3.1. Bottom environment

Export POC flux declined rapidly with depth for the first 1000-m and then declined relatively slowly onto the mid-lower slope and abyssal plain (Fig. 2a). The lowest export POC flux ($2.7\text{--}3.1 \text{ mg C m}^{-2} \text{ day}^{-1}$) was observed on the Sigsbee abyssal plain at depths between 3314 and 3732 m (S1–S5, Table S1). The highest export POC flux ($51.9\text{--}77.7 \text{ mg C m}^{-2} \text{ d}^{-1}$) occurred within the head of the Mississippi Canyon in the NE GoM (MT1 & MT2). Seven out of the ten sites with export POC flux $> 20 \text{ mg C m}^{-2} \text{ d}^{-1}$ were located in the NE GoM (Fig. 1). These high flux sites in the Mississippi (MC) and De Soto Canyon (DC) transects (approximately 700–1000 m) extended deeper than any other transects. As a result, the export POC flux was significantly higher in the NE than in the NW GoM (GAM, region, $n = 51$, $t = 2.57$, $P = 0.013$,

Fig. 2a).

Bottom water temperature dropped dramatically for the first 1500-m from approximately 15 to 4°C and then remained relatively constant onto the lower slope and abyssal plain (Fig. 2b). Bottom dissolved oxygen concentration increased from $\sim 2.5 \text{ mg L}^{-1}$ at the shelf edge to $\sim 4.5 \text{ mg L}^{-1}$ at 2000-m depth and then fluctuated between ~ 4.5 and 5.5 mg L^{-1} on the lower slope and abyssal plain (Fig. 2c). Except for Site S38 along the DC transect, the Shannon diversity indices of sediment grain size varied between 0.7 and 1.1 without an obvious bathymetric pattern (GAM, depth, $n = 51$, $F = 1.58$, $P = 0.195$, Fig. 2d). Site S38 appears to be an outlier with sediment diversity at 0.25. This was due to the extremely high percentage of sand (94.2%) relative to silt (4.1%) and clay (1.6%) in the surface sediments (Table S1). In conclusion, except for the export POC flux, the overall level of bottom temperature, dissolved oxygen concentration and sediment diversity were not statistically different between the NE and NW GoM (GAM, region, $n = 51$, $P > 0.48$)

3.2. Diversity-depth relationship

The observed numbers of species were negatively correlated with depth ($\rho = -0.71$, $P < 0.001$, Table S2). The highest numbers (150–269 species/per site) occupied the east upper to mid slope sites (C7, C4, MT1, MT2, MT4, S35, S36, S42), extending from 481 to 1828 m and the west upper slope site (RW1, W2), extending from 213 to 625 m (Fig. 1, Table S2). The lowest numbers of species (17–26 species/per site) were sampled on the abyssal plain (S1, S2, S3, S4) at around 3600-m water depth.

The species richness, exponential Shannon and inverse Simpson indices were significant parabolic functions of depth (LME, $P < 0.05$, Table 1a). The polynomial relationships predicted that the maximum

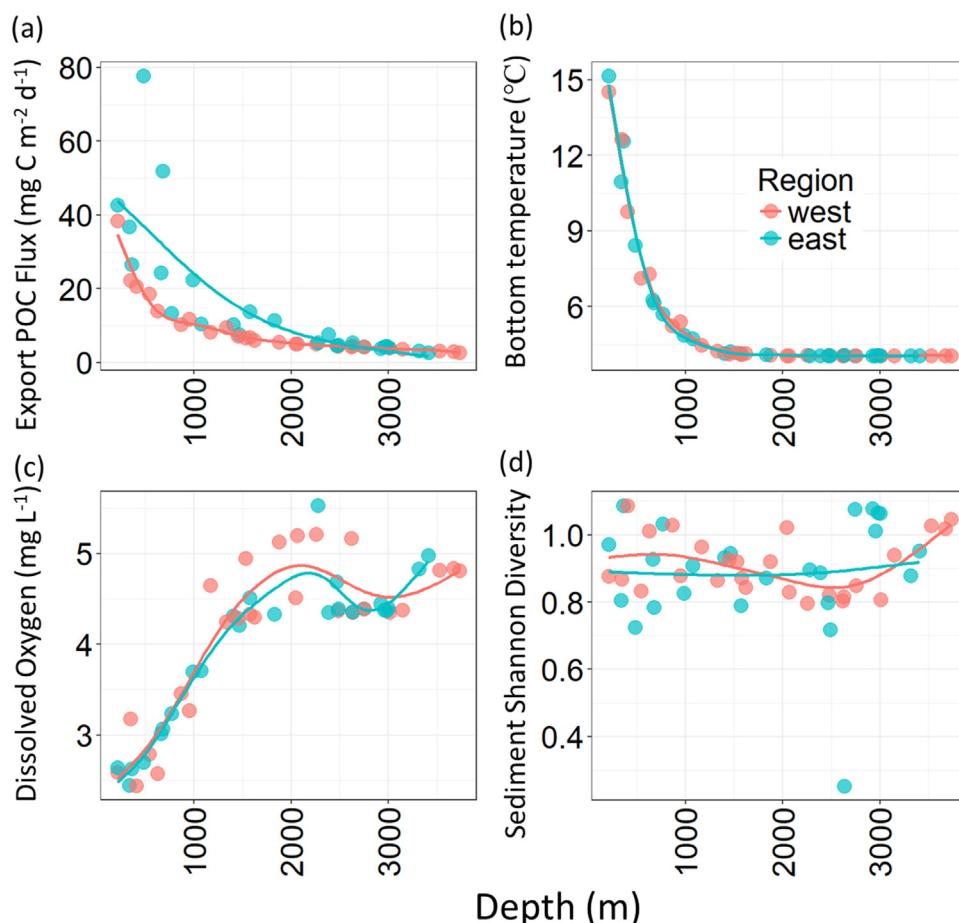


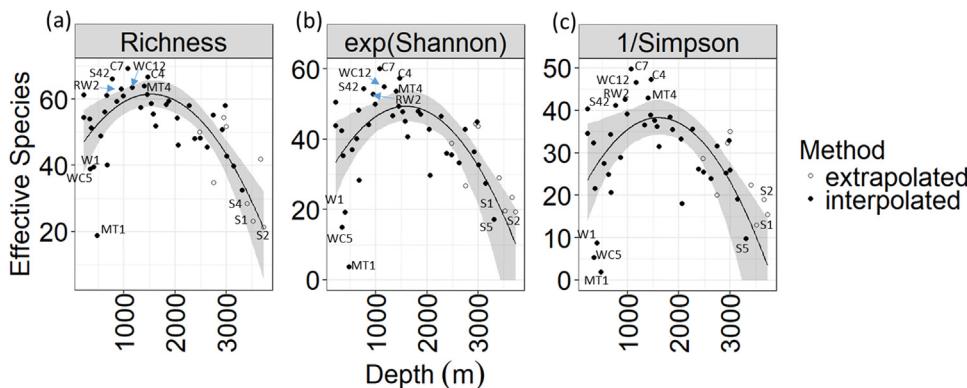
Fig. 2. Bottom environmental conditions during DGoMB sampling in summers 2000–2002. (a) Export POC Flux at the seafloor; (b) bottom temperature; (c) dissolved oxygen concentration; (d) sediment grain size Shannon diversity index calculated from relative proportions of sand, silt and clay fractions. The blue and red lines show the fitted lines by Generalized Additive Model (GAM) for the NE and NW GoM, respectively. The export POC flux data derived from Biggs et al. (2008) and environmental data derived from Jochens and DiMarco (2008). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 1

Regression coefficients for linear mixed effect (LME) and general least square (GLS) models. The basic fixed factors are ‘depth’ and ‘quartic term of depth’. The random factor is ‘transect’ for LME models. Additional fixed factor in individual tests include (b) Basin: basin vs. non-basin, (c) Canyon₁: Mississippi Canyon vs. central slope transects, (d) Canyon₂: east slope vs. De Soto Canyon transect, (e) Region = northeastern vs. northwestern slope separated by 91° latitude and (f) Time: NGoMCS vs DGoMB sampling.

(a) Model	N	Response	Intercept	Depth	Depth ²	
LME	46	Richness	41.6	2.4E-02	*	-1.0E-05 ***
	46	Shannon	27.2	2.6E-02	*	-8.0E-06 **
	46	Simpson	18.0	2.3E-02	*	-7.0E-06 **
(b) Model	N	Response	Intercept	Depth	Depth ²	Basin
	GLS	Richness	109.7	-4.5E-02	1.0E-05	-3.2
		Shannon	93.0	-3.4E-02	0.0E+00	0.9
	(c) Model	Simpson	70.6	-1.9E-02	0.0E+00	4.7
		N	Response	Intercept	Depth	Canyon ₁
		GLS	Richness	15.9	6.1E-02	-1.6E-05 **
			Shannon	0.9	6.8E-02	-1.8E-05 **
			Simpson	-4.0	6.0E-02	-1.6E-05 **
(d) Model	N	Response	Intercept	Depth	Depth ²	Canyon ₂
	GLS	Richness	26.4	4.5E-02	-1.4E-05 **	15.8
		Shannon	20.6	3.3E-02	-1.0E-05 *	12.8
	(e) Model	Simpson	16.3	2.3E-02	-7.0E-06 *	9.4
		N	Response	Intercept	Depth	Region
		GLS	Richness	43.8	1.9E-02	-1.0E-05 ***
			Shannon	28.8	2.1E-02	-7.0E-06 ***
			Simpson	19.4	1.8E-02	-6.0E-06 ***
(f) Model	N	Response	Intercept	Depth	Depth ²	Time
	LME	Richness	44.1	2.1E-02	-1.0E-05 ***	-2.3
		Shannon	29.2	2.3E-02	-7.0E-06 **	-2.4
		Simpson	18.3	2.1E-02	-6.0E-06 **	-2.7

Note: N = numbers of samples, Symbols ‘***’ denotes the coefficients with P-value < 0.001; ‘**’ denotes the coefficients with P-value < 0.01; ‘*’ denotes the coefficients with P-value < 0.05; ‘.’ denotes the coefficients with P-value < 0.01.



diversity occurred at 1535, 1643 and 1684 m (Fig. 3) and on average explained 39.5%, 30.6% and 25% of the total variation, respectively (10-fold cross-validated R^2). The highest species richness, exponential Shannon and inverse Simpson indices occurred on the east (C7, C4, MT4 and S42) and west upper-mid slope sites (RW2, WC12), extending from 767 m to 1463 m (Fig. 1, Fig. 3). The lowest of the three indices occurred either near the edge of the western shelf (W1 and WC5), the head of the Mississippi Canyon (MT1) or on the Sigsbee abyssal plain (S1, S2 and S4 or S5, Fig. 1, Fig. 3).

3.3. Effects of habitat heterogeneity

All three diversity indices were not statistically different between the basin (B1–3) and non-basin slope sites (NB1–NB4) in the west central (WC) transect (GLS, $P > 0.05$, Table 1b, Fig. 4c). There was no detectable difference in the three indices between the Mississippi Canyon (MC) and the adjacent central slope (C) transects (GLS, $P > 0.05$, Table 1c, Fig. 4d, e). Although the species richness was significantly higher on the east (E) slope than on the De Soto Canyon (DC) transect, the exponential Shannon and inverse Simpson indices were not statistically different between the two adjacent habitats (GLS,

Fig. 3. (a) Species richness, (b) exponential Shannon and (c) inverse Simpson indices from 100 randomly selected individuals as function of depth in the Northern Gulf of Mexico (GoM). The fitted line shows the mean population-level (fixed-factor-levels) prediction of general linear mixed-effect model (LME) from 1000 bootstrap resampling. The shaded area indicates 2.5–97.5 percentiles of the bootstrap predictions. The symbols indicate the mean diversity, whether interpolated (closed symbol) or extrapolated (open symbol) to the diversity of 100 randomly selected individuals. Note that the shaded area below zero was not shown.

Table 1d, Fig. 4f, g). The overall level of diversity was significantly higher on the northeastern (C, E) than the northwestern slope transects (RW, W, WC) (GLS, $P < 0.05$, Table 1e, Fig. 5).

3.4. Comparison with historical sampling

All three diversity indices were not statistically different between the current (DGoMB) and historical (NGoMCS) sampling across west (W), west central (WC), central (C) and east (E) slope transects (LME, $P > 0.05$, Table 1f, Fig. 6).

3.5. Relative importance of environmental drivers

Monotonic and quadratic terms of export POC flux were the only environmental variables that significantly explained all three diversity indices (average LME, $P < 0.01$, Table 2) with 100% likelihood to be included in the LME models (relative importance, Table 2). The relative importance (likelihood to be included in models) of dissolved oxygen (DO), temperature (Temp) and sediment diversity (Sed Div) ranged from 44% to 76%, 27–46% to 44–47%, respectively. Although no statistical linear effect was evident for DO, Temp and Sed Div, separate

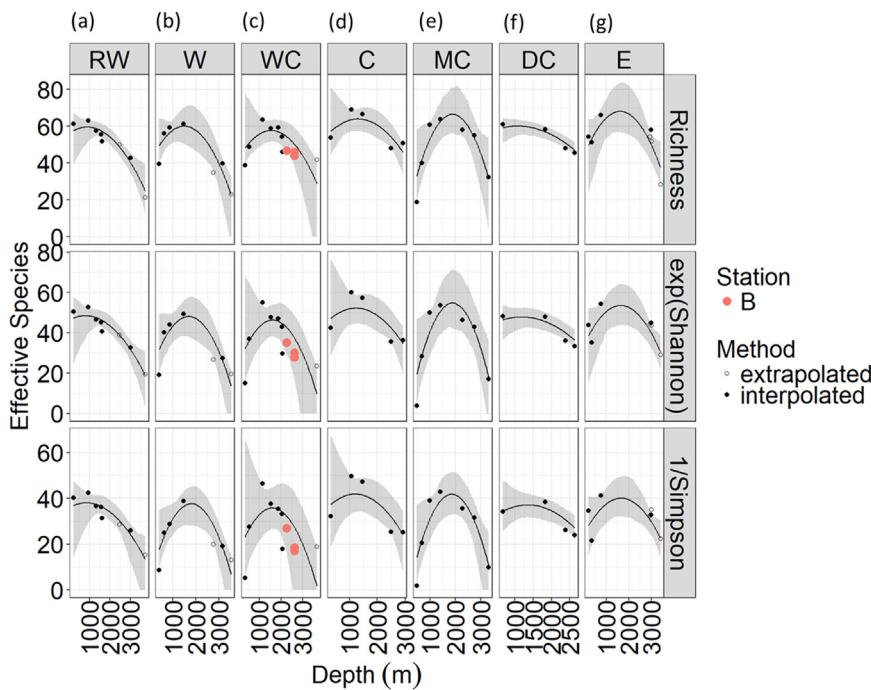


Fig. 4. Species richness, exponential Shannon and inverse Simpson indices from 100 randomly selected individuals as a function of depth across (a) real west, (b) west, (c) west central, (d) central, (e) Mississippi Canyon transect, (f) De Soto Canyon and (g) east transects in the Northern Gulf of Mexico (GoM). The fitted line is the mean transect-level (random-factor-level) prediction of the general linear mixed-effect model (LME) from 1000 bootstrap re-samplings. The shaded area is the 2.5–97.5 percentiles of the bootstrap predictions. The symbols indicate the mean diversity, whether interpolated (closed symbol) or extrapolated (open symbol) to the diversity of 100 randomly selected individuals. The red symbols indicate the three basin sites (B1 to B3) for comparison with the west central (WC) slope transect.

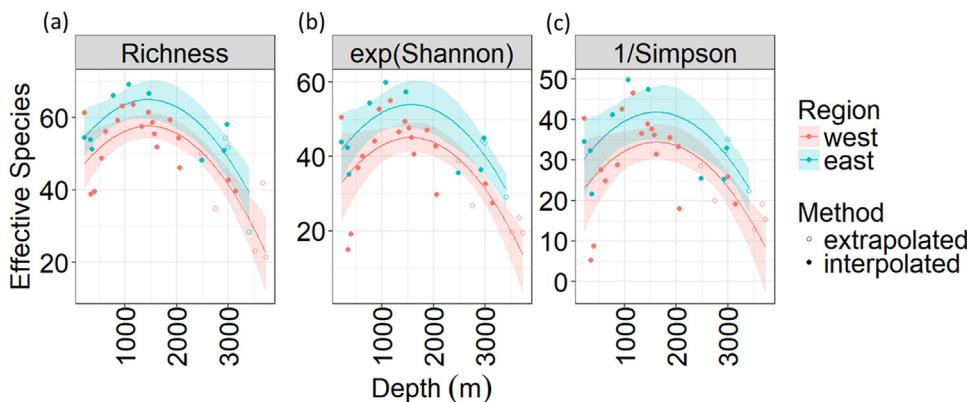


Fig. 5. (a) Species richness, (b) exponential Shannon and (c) inverse Simpson indices from 100 randomly selected individuals as a function of depth between the northwestern and northeastern slope. The fitted line is the mean prediction of the general least square (GLS) model from 1000 bootstrap re-samplings. The shaded area is the 2.5–97.5 percentiles of the bootstrap predictions. The symbol indicates the mean diversity, whether interpolated (closed symbol) or extrapolated (open symbol) to the diversity of 100 randomly selected individuals.

analysis based on GAMM suggests that the export POC flux, temperature and sediment Shannon diversity were significant smooth (non-linear) functions of all three indices (Table 3). Dissolved oxygen had no effect either in the LME or GAMM, likely because our sampling sites were never subjected to hypoxic conditions ($< 2 \text{ mg L}^{-1}$, Fig. 2c). The contribution of export POC flux to the fitted diversity was the lowest at $2.7 \text{ mg C m}^{-2} \text{ day}^{-1}$ on the Sigsbee Abyssal Plain and $77.7 \text{ mg C m}^{-2} \text{ day}^{-1}$

within the head of the Mississippi Canyon (Fig. 7a–c). The tipping point where the diversity indices start to decline on both sides ranged from 13 to $32 \text{ mg C m}^{-2} \text{ day}^{-1}$. The predicted diversity declined with temperature from approximately 4 to 10°C and then increased slightly from approximately 10 to 15°C (Fig. 7d–f); however, the majority of the data were concentrated around 4°C and thus the model uncertainty increased toward the higher temperature range. When Site S38 (outlier)

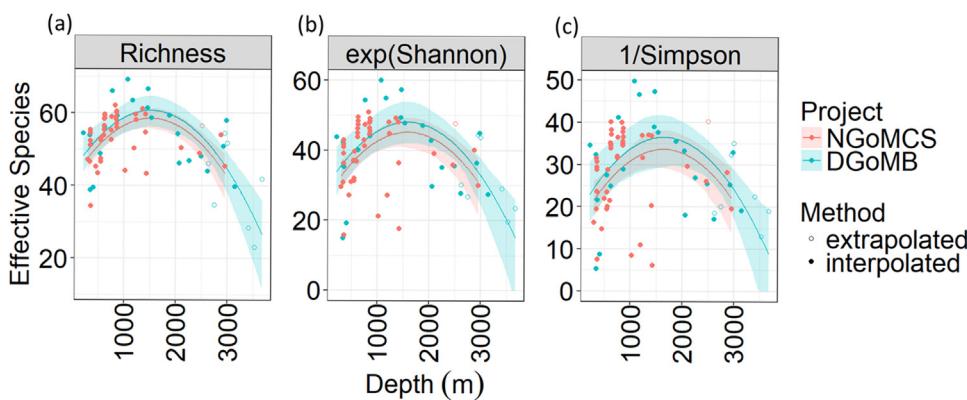


Fig. 6. (a) Species richness, (b) exponential Shannon and (c) inverse Simpson indices from 100 randomly selected individuals as function of depth during the NGoMCS and DGoMB studies in the northern Gulf of Mexico (GoM). The fitted line is the predicted mean of the general linear mixed-effect model (LME) from 1000 bootstrap resamplings. The shaded area is bounded by the 2.5–97.5 percentiles of the bootstrap predictions. The symbol indicates the mean diversity, whether interpolated (closed symbol) or extrapolated (open symbol) to the diversity from 100 randomly selected individuals.

Table 2

Regression coefficients (a) and relative importance (b) of fixed factors from the multi-model averaging of linear mixed effect (LME) models during DGoMB project.

Model	N	Response	Intercept	E POC	E POC ²	DO	Temp	Sed Div
(a) LME Average	48	Richness	59.6	***	11.1	***	-9.3	***
	48	Shannon	47.3	***	11.8	**	-8.6	***
	48	Simpson	35.7	***	11.2	**	-6.7	***
(a) Relative importance		Richness		1		1	0.44	0.27
		Shannon		1		1	0.65	0.41
		Simpson		1		1	0.76	0.46

Note: N = numbers of samples, E POC = export POC flux, DO = dissolved oxygen concentration, Temp = temperature, Sed Div = sediment grain size Shannon diversity index. Symbols '***' denotes the coefficients with P-value < 0.001; '**' denotes the coefficients with P-value < 0.01; '*' denotes the coefficients with P-value < 0.05; '.' denotes the coefficients with P-value < 0.01.

Table 3

Results of Generalized Additive Mixed Effect Model (GAMM) for species richness, exponential Shannon and inversed Simpson indices from 100 random selected individuals.

	Richness	Shannon	Simpson
Intercept			
Estimate coef	50.3	38.5	28.7
t value	31.7	19.0	13.6
P value	2.0E-16	***	2.0E-16
E POC			
Estimate df	5.8	5.4	3.3
F value	21.5	13.8	7.1
P value	2.0E-16	***	2.0E-16
Temp			
Estimate df	2.1	2.3	2.4
F value	1.3	2.7	2.9
P value	4.3E-03	**	5.6E-05
DO			
Estimate df	0	0	0
F value	0	0	0
P value	0.55	0.47	0.53
Sed Div			
Estimate df	2.1	2.6	2.3
F value	1.8	2.0	1.5
P value	4.1E-04	***	4.3E-04
R ² (adj)	0.78	0.70	0.59
N	48	48	48

Note: N = numbers of samples, E POC = export POC flux, DO = dissolved oxygen concentration, Temp = temperature, Sed Div = sediment grain size Shannon diversity index. Symbols '***' denotes the coefficients with P-value < 0.001; '**' denotes the coefficients with P-value < 0.01; '*' denotes the coefficients with P-value < 0.05; '.' denotes the coefficients with P-value < 0.01.

was removed, the predicted diversity increased with sediment grain size diversity from values of approximately 0.7–0.9, past which the contribution to fitted diversity remained stable or dropped slightly (Fig. 7g-i).

4. Discussion

4.1. Productivity

This analysis supports the idea that α -diversity is suppressed when resources are high, it attains a maximum at some intermediate level of resource availability, but then declines when resources become limiting. Several investigations along the western North Atlantic margin also show such distinct mid-depth diversity maximum (MDM) (Hessler and Sanders, 1967; Maciolek and Smith, 2009; Rex, 1981). The diversity values in these reports were plotted as a function of estimated POC input to the seafloor (Fig S1). The MDM for this assemblage of curves ranged from 8.5 to 16.9 mg C m⁻² d⁻¹, which are comparable to the range in our study. The MDM however was substantially deeper in the Atlantic (1.4 vs. 2 km) due, we believe, to the higher primary production rate along the western Atlantic margin. This supports our suggestion that the MDM is related to the POC input (Rex and Etter,

2010).

The actual causative relationships nevertheless between POC input and the inferred competition among the resident species remain complex. Here we modified a conceptual diagram of Rex and Etter (2010) by coupling our observed Hill's number ($q = 0$) with total density of macrofauna (derived from Wei et al., 2012a) and export POC flux at the seafloor (derived from Biggs et al., 2008) to explain the productivity-diversity relationship (Fig. 8). The 30 or so species per 100 individuals supported by the POC flux of ca 3 mg C m⁻² day⁻¹ coexisted among 800–1600 individuals per square meter on the abyssal plain. The low population density on the abyssal plain implies that the communities may be more prone to extinction from stochastic events (McClain and Schlacher, 2015). Likewise the diversity might be maintained by constant migrations from bathyal source populations (Rex et al., 2005; Stuart et al., 2016; Wei et al., 2010). We cannot however rule out mechanisms such as a decrease of specialists, consumers or species with high metabolic demands in food-limited conditions (McClain and Schlacher, 2015). The increasing nestedness with depth in the N GoM suggests that the abyssal-sink hypothesis might be the dominant mechanism structuring the macrofaunal communities on the Sigsbee Abyssal Plain (Stuart et al., 2016; Wei et al., 2010). From the abyssal plain back up the continental slope, species accumulate as food becomes more available. The parabola approaches maximum at estimated POC fluxes of 8–38 mg C m⁻² day⁻¹, which supports densities of approximately 3,400–11,000 individuals m⁻², with more than 60 species coexisting per 100 individuals in a sample. The inverse relationship between the diversity and the population density on the shallow descending limb of the curve has been attributed to competitive exclusion (Huston, 1979; McClain and Schlacher, 2015; Rex, 1981; Rex and Etter, 2010), because substantial POC is available (40–80 mg C m⁻² day⁻¹) to support high animal density (6,800–22,000 individuals m⁻²), in our case, the upper slope and the head of the Mississippi Canyon. The lowest diversity at the shallow extreme was produced by dominance of the amphipod *Ampelisca mississippiana* within the head of the Mississippi Canyon (Soliman and Rowe, 2008). As this species' dominance diminished offshore, the evenness increased, along with the Hill's number per 100 individuals.

4.2. Diversity at the head of Mississippi Canyon

The exceptionally low diversity (both richness and evenness, this study), high abundance (Wei et al., 2012a) and distinct species composition (Wei et al., 2010) of macrobenthos at the head of the Mississippi Canyon were probably a function of rapid accumulation of organic material from the Mississippi River and the adjacent continental shelf. Indeed, we found macrophyte debris in separate trawl samples, including water hyacinth (23 clumps, length < 6 in.), Sargassum, and wood fragments of all sizes, presumably originating in the Mississippi river plume (Wei et al., 2012b). The enhanced infaunal stocks therefore may be linked to organic enrichment due to the accumulation of macrophytes or lateral transport of detritus (De Leo et al., 2010; Vetter and Dayton, 1998; Wei et al., 2012a). These enrichment patches may

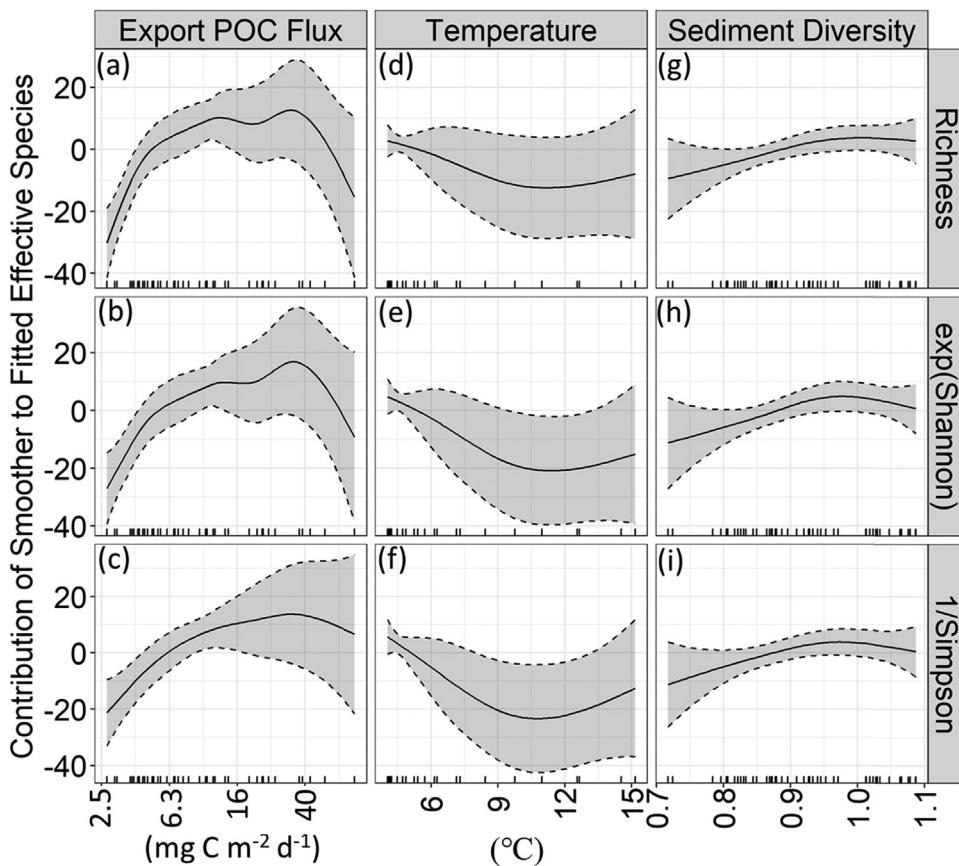


Fig. 7. Contribution of export POC flux (a-c), temperature (d-f) and sediment diversity (g-i) to fitted species richness, exponential Shannon and inverse Simpson indices. Each diversity index was calculated from 100 randomly selected individuals and the models were fitted by the generalized additive mixed effect model (GAMM). The solid and dashed lines are the smooth component and 95% confidence intervals of the GAMM. The rugs along the bottom illustrate the distribution of environmental values.

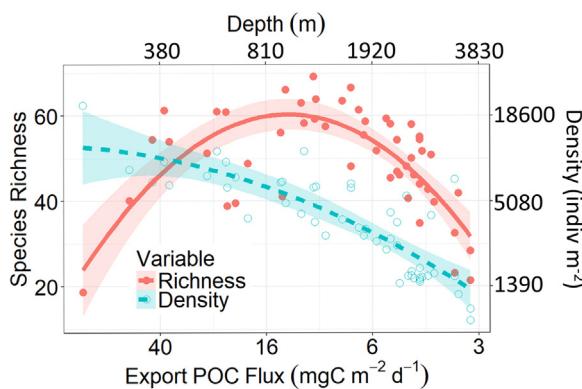


Fig. 8. Unimodal diversity-productivity model in relation to animal density and sampling depths. The diagram follows a conceptual model of Rex and Etter (2010) with the empirical curve fits. The top x-axis is approximate depth corresponding to the labels on the bottom POC axis (from Fig. 2a). The bottom and right axes are in log scale. The density data are taken from Wei et al. (2012a).

provide microhabitat in which opportunistic species can take advantage of the favorable resources during the early stage of succession (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1996). It might be inferred that the dominance of the tube building amphipod *Ampelisca mississippiensis* is related to competitive interference in feeding and movement of other benthic organisms, as demonstrated by Mills (1969) in *A. abdita*. In the latter species, periodic destruction of the tube mat opened up space for recruitment of the snail *Ilyanassa obsoleta*, resulting in an oscillating pattern of community dominance. The numerous rare species that coexist with the amphipod may be colonists in disturbed areas or small associated animals that live on or between the tubes.

Canyon habitats likely experience mass wasting events triggered by river flushing, storm surges, earthquakes, or down-slope currents

(Coleman and Prior, 1988; Gardner, 1989; Inman et al., 1976; Okey, 1997; Puig et al., 2004; Ross et al., 2009; Shepard et al., 1974), which can cause localized mortalities. Other physical disturbances, such as strong bed flows driven by internal tides or seasonal storm-induced sediment flushing, have been suggested to be responsible for low diversity and high dominance of macrobenthos in canyons (Gage et al., 1995; Liao et al., 2017; Okey, 1997). Nevertheless, it remains uncertain whether the organic enrichment or the physical disturbance caused the low diversity at the head of Mississippi Canyon. Given the high total numbers of species at the canyon head (163 species, ranks 9th out of all stations), any potential catastrophic events there have not caused chronic extinctions.

4.3. Habitat heterogeneity

There was little evidence that the overall level of α -diversity in bathymetric depressions (e.g., mesoscale salt basins and submarine canyons) differed from the diversity on the adjacent slope. However, (1) elevated infauna biomass in the mesoscale basins and submarine canyons (i.e. the Mississippi and De Soto, Wei et al., 2012a), (2) excess organic inputs for the canyon head food web (Rowe et al., 2008b), (3) submergence of assemblages following the canyon feature (Wei et al., 2010), (4) decreasing diversity due the organic accumulation and competitive interference at the canyon head (this study), and (5) increasing litter deposition near or in the canyons (Wei et al., 2012b) all suggest that topographic depressions may be active traps, funnels and conduits of terrestrial and marine organic materials and debris in the deep GoM. The shapes of the unimodal diversity-depth pattern however differed between the submarine canyon (Fig. 4e, f) and the adjacent slope (Fig. 4d, g). Perhaps the overall level of α -diversity was not as responsive as standing stocks and composition. In an energetic submarine canyon off SW Taiwan, strong bed flows driven by internal tides appear to alter all aspects of community structure including the

diversity of higher taxa (Liao et al., 2017).

The overall level of α -diversity on the NE GoM slope (excluding submarine canyons) was significantly higher than the diversity on the NW GoM slope, even though mesoscale habitat heterogeneity (i.e., salt basin, canyons) had seemingly little effect. Interestingly, such east-west variation in diversity was not evident when the two large canyons (i.e., the Mississippi and De Soto) were included in the NE GoM for comparison (result not shown here). This is probably due to the low diversity at the Mississippi Canyon head (Site MT1) and on the deep-sea sediment fan (Site S5). These extremes smother the east-west variation in overall levels (Fig. 4e).

Biggs et al. (2008) described a seasonal variation of sea surface chlorophyll concentration (SSC) associated with mesoscale eddies in the northeastern GoM. In three summers during the DGoMB sampling, these eddies transported the low salinity, high chlorophyll Mississippi River plume water off the shelf into the deep eastern GoM, contributing to more than 50% increase in SSC in June–August over November–February in the NE GoM and approximately 3-fold increase of yearly average SSC and a 2-fold increase of sinking export POC flux at seafloor in the NE over NW GoM (Fig. 2a). The higher food supply from sinking phytodetritus in the NE GoM, to some degree, likely contributed to the high α -diversity because we observed little east-west variation in temperature, dissolved oxygen and sediment size diversity (Fig. 2b, c, d).

The export POC flux however was probably not the only factor, because if it were, the higher flux gradient on the NE GoM seafloor should shift the tipping point of the mid-depth diversity maximum (MDM) to a deeper depth (Rex and Etter, 2010), instead of elevating the overall level of diversity (i.e., shifting the MDM upward). We hypothesize that the diverse habitats (large canyons, steep escarpments, cold seeps and deepwater corals in the NE GoM) may provide additional ecological niches that enhance diversity. In fact, the satellite-based export POC flux used here does not consider the role of lateral transport of organic matter at depth along the sea floor (Biggs et al., 2008). The delivery of detritus to the NE GoM seafloor through vertical sinking and lateral transport by canyons and down along the Mississippi sediment fan are much more complex than the flux model suggests. Thus the flux estimates in Fig. 2a should be considered as the surface contribution of organic carbon to the gently sloping seafloor, excluding any influence of hydrodynamics and morphological features. It is also possible that the lateral down-slope transport of organics by submarine canyons provides subsidy to the slope habitat and thus sustains the higher level of diversity on the NE GoM slope.

4.4. Temperature, sediment heterogeneity and evolutionary history

We found that the diversity-temperature relationship was non-linear and appeared to be negative at the lower temperature range (approximately 4–10 °C). This pattern does not support the recent synthesis of deep-sea diversity-temperature relationships by Yasuhara and Danovaro (2016), in which “a gradual diversity increase at low temperature (< 10 °C), a maximum at intermediate temperature (~ 10–15 °C), and rapid decline in high temperature (> 15 °C)”. We suspect that a positive diversity-temperature relationship in the cold temperature range is smothered by the increasing diversity with decreasing export POC flux along the shallow extension of the MDM parabola. The two forces operate in opposite directions and the effect of export POC flux overwhelms the effect of temperature (McClain et al., 2012; Tittensor et al., 2011).

The effect of sediment diversity was non-linear and minimal compared to the export POC flux. Nevertheless, we acknowledge that a slight positive relationship between α -diversity and the lower extreme of sediment diversity was apparent when the outlier Station S38 (with very low sediment diversity, Fig. 1d) is removed from the analysis. With Station S38 included, neither the linear model nor the additive model detected an effect of sediment.

It has been suggested that the deep Gulf of Mexico may have suffered a geologically recent extinction event (i.e., dysoxia or anoxia), based on the non-equilibrium, wide depth ranges of isopod crustaceans (Wilson, 2008). The more comprehensive taxonomic coverage by Wei et al. (2010) and high nestedness of polychaete distribution (Stuart et al., 2016) provide little additional information to refute this suggestion. Thus, the decline in species past the depth of the tipping point of MDM may be a function of on-going processes to re-populated the deep basin (Wilson, 2008), and not a lack of food.

5. Conclusions

Significant Mid-Depth Maxima (MDM) in α -diversity patterns were observed in seven parallel transects cutting across the continental margin and abyssal plain in the northern Gulf of Mexico. The unimodal diversity patterns had minima at high export POC flux on the upper continental slope and on the abyssal plain with extremely low input of POC, with maximum diversities at intermediate levels of biomass and input of POC. Macrofauna α -diversity was not statistically different between the meso-scale basins in NW GoM or submarine canyons (the Mississippi or De Soto) in the NE GoM and their respective adjacent slope habitats, although the overall lowest diversity was encountered in the Mississippi Canyon that was dominated by a single species of amphipod. Among the normal, gently sloping transects, the α -diversity in the NE GoM was significantly higher than that in the NW GoM, which may reflect elevated export POC flux from sinking phytodetritus related to the mesoscale eddies and the lateral transport of organics from the Mississippi River, Mississippi and De Soto Submarine Canyons in the NE GoM. Because all sampling was conducted along similar depth intervals and ranges, this finding confirms that there is a direct link between productivity and diversity, independent of the depth effect.

A comparison of taxa and transects between the large-scale sampling in the 1980's (NGoMCS) and in the 2000's (DGoMB) illustrates that the parabolic pattern and maximum elevation of macrofauna α -diversity with depth remained stable over the 20-year period. These two studies 20 years apart have provided one of the most intensive and comprehensive deep-sea macrofauna datasets to date. Our findings provide a foundation for predicting the possible responses of deep-sea α -diversity to climate change (through changing productivity and temperature) and serve as an ecological baseline against which anthropogenic impacts in the deep sea (i.e., BP Deepwater Horizon Oil Spill in 2010) can be compared.

CRediT authorship contribution statement

Chih-Lin Wei: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Gilbert T. Rowe:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing.

Acknowledgements

For macrofauna species identification, we thank G. Fain Hubbard and Yuning Wang (polychaetes), George D. F. Wilson (isopods), John M. Foster and Yousria Soliman (amphipods), Roe Davenport, Mary K. Wicksten and Min Chen (bivalves), Iorgu Petrescu (cumaceans), and Amélie H. Scheltema (aplacophorans). We also thank Archie Ammons, Clifton Nunnally, Lindsey Loughry, Matt Ziegler, and Xiaojia Chen, Min Chen, Yuning Wang, and Yousria Soliman for sample sorting. We thank Captain Dana Dyer and the men and women onboard R/V Gyre for their assistance. This research was funded by the US Department of Interior, Minerals Management Service, Contract No 1435-01-99-CT-30991. This paper is a contribution of the Continental Margin Ecosystems (COMARGE) component of the Census of Marine Life (CoML) supported

by the Sloan Foundation. The preparation of this paper was funded by Ministry of Science and Technology, Taiwan (107-2611-M-002 -012).

Author contributions

GTR designed the study. GTR oversaw the collection of the data and CLW performed the analyses. CLW and GTR wrote the paper and contributed to M.S. analysis.

Data accessibility statement

All biological and environmental data are available from the Environmental Studies Program Information System (ESPIS) of the Bureau of Ocean Energy Management (BOEM).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dsr.2018.12.005](https://doi.org/10.1016/j.dsr.2018.12.005).

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